

Climbing Plants in Relation to their Supports in a Stand of Dry Rainforest in the Hunter Valley, New South Wales

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Climber individuals from twenty-six native species were sampled across a stand of dry rainforest in the lower Hunter Valley and a series of observations and measurements was carried out on each climber and its support(s). Emphasis was placed on the woody climbers (= lianes) present. The aim was to describe how woody climbers fit into the structure imposed by trees and shrubs. The climbers were observed to have some support preferences in terms both of support size (depending on the climbing mechanism employed) and of support species. Shade-tolerant and light-demanding liane species could be recognised. Liane species were found to differ in their ability to spread from support to support and also in the disposition of their foliage on their support(s). All but two of the lianes were observed to produce seedlings; differences were noted between species in the potential for vegetative reproduction. It was apparent that the vertical and horizontal distribution (at a scale of a few metres) of liane species within this stand is strongly influenced by the local forest structure and the growth characteristics of the individual liane species.

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INTRODUCTION

The species diversity of climbing plants diminishes outside the lowland tropics, but they are still a significant component of most lowland rainforest types in the 30°s of latitude in the southern hemisphere. In the rainforest vegetation of eastern Australia, liane (woody climber) species richness is greatest in the tropical humid conditions of the latitude band 16-18°S and decreases with increasing latitude (Webb, 1968). Although lianes contribute only about 1-6% of the total above-ground biomass in moist tropical forests, they have been shown to make a very substantial contribution to the foliage of the canopy and thence to litter production (Putz, 1983). In Australia, Hegarty (1988) found that they contributed about 24% of all leaf litter in a rainforest stand near Brisbane.

The climbing habit is a derived one, being characteristic of some of the later families in the fossil record and has developed independently in many taxa (Hegarty, 1989). Its evolution in so many unrelated groups suggests that there are strong selective pressures favouring it in tropical plant communities with closed canopies, and competition for light is certainly one of these main pressures (Gentry, 1985). In NSW native rainforest climbing plants are found within more than forty families, representing about seventy genera and 120 species, roughly 30% of the number of native rainforest trees and shrubs in the same state (Williams, 1979).

The epiphytic, strangler and climber growth forms often grade into each other over the life of an individual (Richards, 1952; Kelly, 1985). Stranglers have been excluded from this present study but a small climbing fern (*Arthropteris tenella*) (Forster. f.) Smith, usually regarded as an epiphyte and lithophyte, has been included. A distinction will be made between lianes (woody climbers) and thin wiry climbers (stem diameter usually less than 1 cm).

Trellis (support) requirements and forest structure influence the distribution of lianes in the forest and an individual's probability of reaching the canopy. Trellis availability was found to be a major factor controlling liane access to the forest canopy (Putz, 1984a; Hara, 1987). Thus, lianes are more likely to reach the canopy via the edges of treefall gaps, where closely-spaced, small-diameter supports (tree and liane stems) are abundant, than from the primary-forest floor (Penalosa, 1983; Putz, *ibid.*). However, climbing plants do not necessarily have to reach the canopy to be successful. There are shade-tolerant and light-demanding species (Grubb *et al.*, 1963); the majority of thin wiry climbers belong to the former group and go through life shaded in the understorey.

The dependence of climbers on other plants for support means that the possession of specialised organs, to assist in climbing, may be advantageous. Four main climbing mechanisms are recognised:

- 1) *Tendrils*: modified leaves, leaflets, inflorescences or stipules twine around a support;
- 2) *Root climbers and adhesive-tendrils*: attached to sides of the support with glandular secretions or by growing into crevices;
- 3) *Twiners*: the apical portion of the shoot, the branches, or petioles twine around the support;
- 4) *Scramblers and hook climbers*: lean on but do not become closely attached to the support.

The main aim of this present study is to describe how individual native climber species fit into the three-dimensional structure of the rainforest in which they occur. Are there recognisable differences amongst species, in terms of micro-habitat preferences within that three-dimensional structure? What are some of the growth characteristics enabling climbers to obtain a favourable position for photosynthesis? A stand of dry rainforest was selected for study at Moonabung Falls (32°36' S/151°31' E), 10 km west of Paterson and 45 km north west of Newcastle. For a description of the dry rainforest sub-formation see Williams *et al.* (1984). This rainforest type commonly has a rich and abundant climber component. Some other aspects of the Moonabung Falls stand have recently been examined by Vernon (1985) and Doyle (1990).

STUDY SITE

The Moonabung stand is confined to the slopes of a shallow gorge within which two streams join (Moonabung and Webbers Creeks). The upstream boundaries of the stand are delimited by falls on each creek. Most of it is situated on the south-facing side of the gorge; only this part was sampled in the present study, an area of about 13 ha in a total of 19 ha. The altitude ranges from 55 m to 125 m.

The area is underlain by the Paterson Volcanics, which are of Carboniferous age and consist of acid crystal tuffs, conglomerate, sandstone and acid lavas. The soils of the study area have formed mainly from rhyodacite. They are predominantly skeletal and, according to Vernon (1985), are of low-to-medium fertility (oligotrophic to mesotrophic). A late-summer rainfall peak dominates the yearly distribution (Bridgman, 1984) and average annual rainfall was estimated to be about 1000 mm at Moonabung Falls by Vernon (*ibid.*).

The stand is considered to be mature in composition and structure, and very largely free of disturbance except for the invasion of the shrub/scrambler, *Lantana camara* L. Using the structural/physiognomic classification developed by Webb (1968, 1978), Moonabung was classified by Vernon (1985) as simple notophyll low vine forest

(SNLVF). The canopy is uneven and ranges from 14 to 18 m in height. Scattered emergents (mainly *Ficus macrophylla* Dest. ex Pers.) of 20 to 25 m in height are present and there is a discontinuous small tree layer from 5 to 8 m. The shrub layer is sparse and consists of only a few species. *Lantana camara* is abundant only in the larger canopy gaps and at the edges of the stand. Vernon found the most abundant tree species to be *Mallotus philippensis* (Lam.) Muell. Arg., followed by *Drypetes australasica* (Muell. Arg.) Pax and K. Hoffm and *Streblus brunonianus* (Endl.) F. Muell. and she assigned the stand to the *Drypetes*–*Araucaria* Alliance and to the *Ficus* spp. – *Streblus*–*Dendrocnide*–*Cassine* Suballiance proposed by Floyd (1990). For this stand she found an overall mean basal area of 47 m²/ha for tree stems ≥ 10.0 cm gbh (girth at breast height, 1.4 m).

METHODS

The main sampling requirement was the objective selection of a reasonably large sample (hundreds) of native climbers from across the stand. To address the main aims of the project, a series of observations and measurements was carried out on each climber and its support(s). At the same time, it was desirable to provide across-stand estimates of climber density and basal area because there is a lack of this kind of basic information for climbing plants in Australia. A plotless method of sampling would allow these two needs to be fulfilled. The point-centred quarter method was chosen because, of those plotless methods available, it is usually regarded as the most efficient (Cottam and Curtis, 1956). As a start, ten points were randomly selected from the points of intersection defined by a right-angled grid system (25 m x 100 m) across the stand. Only the nearest climber in each quarter was utilised for the density and basal area estimates. Such a restricted choice is an integral part of this plotless method. For the other measurements however, a larger sample was obtained (but one based on the objective framework provided by sampling for the quarter method) by selecting the five nearest individuals.

More climber species were encountered than the thirteen species expected on the basis of a previous study by Vernon (1985) and twelve additional grid points were later randomly chosen to increase the number of points for the climber density and basal area estimates to twenty-two. Stem circumference measurements at the point of emergence from the soil were used for basal area estimates. Any randomly-chosen grid point that fell into an area heavily infested with *Lantana camara* was excluded and another random point selected. As a result of this exclusion criterion it is believed that the larger canopy gaps may have been undersampled.

In each of the four quarters of the ten initially-chosen points, the stems of the five closest adult climbers were followed, regardless of extent, and measurements (see below) of each support utilised by the individual climber were recorded. A climber was regarded as one individual even if additional roots formed along its stem(s), as long as the stem system clearly remained alive between the rooting points. Thin wiry climbers were separated into climbing (adult) and non-climbing (seedling) individuals (following Putz, 1984a) and lianes were separated into ≥ 1.0 cm stem-diameter (adult) and < 1.0 cm stem-diameter (seedling) individuals. For each adult climber the following observations and measurements were taken:

- 1) Identification of climber species
- 2) Emergence diameter (or circumference) of the climber – within 10 cm of the point of initial emergence from the ground
- 3) Ascent diameter (or circumference) of the climber – stem diameter at breast height (dbh), approximately 1.4 m above the ground

- 4) Identification of support species
- 5) Support (tree or sometimes a liane) diameter (or circumference) at breast height
- 6) Estimated height of the support(s) (to the nearest 0.5 m)
- 7) Direct distance from the nearest rooting point to the centre of the base of the next support (to the nearest 0.1 m). The nearest rooting point could have been either the point of initial emergence or a secondary rooting point, either on the way to the first support or between successive supports
- 8) Number of secondary rooting points along the stem(s)
- 9) Maximum height reached by the climber on each of its supports (to the nearest 0.5 m).

The five nearest climber seedlings in each quarter were also selected at the same ten grid points. Each plant was identified and stem diameter, seedling height and length were measured.

RESULTS

Some Basic Features

At least twenty-seven climber species are present in the Moonabung rainforest stand, representing seventeen families and twenty-five genera (Appendix). At Moonabung, the density of adult native climber individuals was estimated to be 520/ha, while the density of seedlings was estimated as 7950/ha. In the same stand, Vernon (1985) found a mean tree density (stems ≥ 3.2 cm dbh or 10.0 cm girth) of 1870/ha. The relative abundances of the main species are also set out in the Appendix. An across-stand Importance Value (IV) has been used as an index of abundance. In the calculation of this IV across all eighty-eight of the sampled quarters, relative numbers, frequency

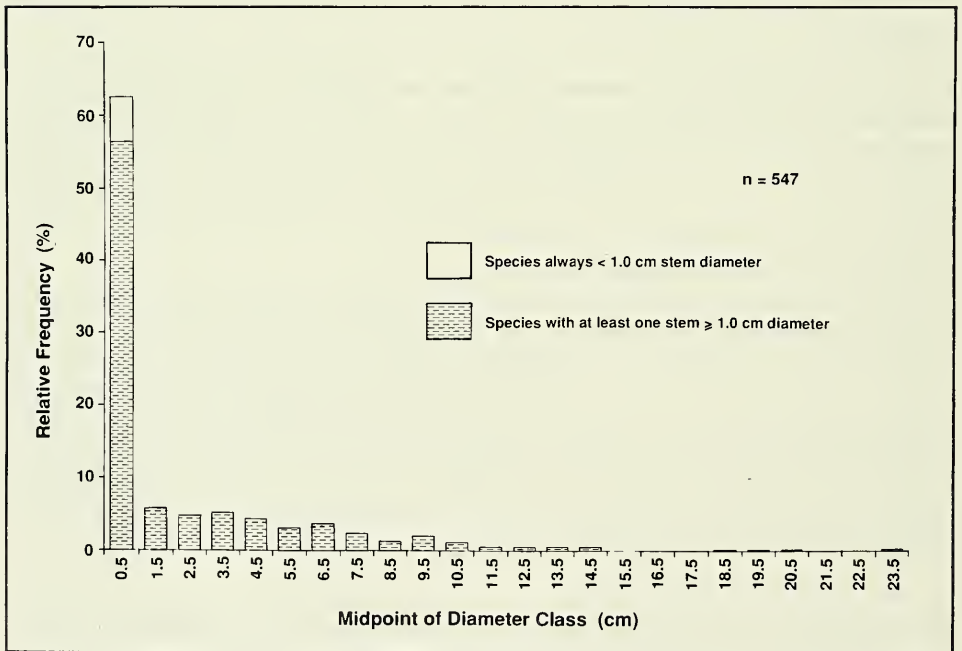


Fig. 1. Frequency distribution of emergence stem diameters for all native climber species within the Moonabung rainforest stand.

and stem basal area have been given equal weight. *Austrosteenisia blackii* (F. Muell.) Gees has the greatest across-stand IV of the climber species within the stand followed by *Parsonsia straminea* (R. Br.) F. Muell.

The liane species in the study area have a wide representation in NSW, both in an overall spatial (north-to-south) sense and across rainforest types. The ten species examined hereafter in some detail are common in dry rainforest, nine of them (excluding *Morinda acutifolia*) also occur in the subtropical rainforest subformation and some of them even in warm temperate (four species) and cool temperate (two species) rainforests (Williams, 1979).

The frequency distribution of stem diameters of all native climber individuals is shown in Fig. 1. The abundance of climbers in the smallest diameter class indicates that, as a group, climbers are presently developing in large numbers to the seedling stage in the rainforest understorey. Individual frequency distributions of the more common woody species show weakly bimodal size distributions (Chalmers, 1991). This pattern is masked in Fig. 1 by the differences in stem size between species, i.e. the second peak of the smaller liane species overlaps the trough of the larger liane species. Doyle (1990) found that the strangler figs (*Ficus macrophylla* and *Ficus superba* Miq.) in the Moonabung rainforest stand have a bimodal distribution pattern.

The frequencies of the different climbing mechanisms used by the climbers at Moonabung are presented in Table 1. Twining is the most common mechanism, in terms of both number of species and number of individuals. The predominance of the twining mechanism was also reported by Putz and Chai (1987) in Sarawak and by Hegarty (1988) in south-east Queensland. The main climbing mechanism of each of the climbers at Moonabung is given in the Appendix.

Several species use a combination of climbing mechanisms simultaneously, or in a sequence. Three of the twiners, *Ripogonum album* R. Br., *Malaisia scandens* (Lour.) Planch subsp. *scandens* and *Parsonsia velutina* R. Br. have prickles or hooks along their twining stems. In contrast to the sturdy prickles of *R. album*, the minute hooks on the leaders of *M. scandens* subsp. *scandens* (also noted by Cribb, 1985 and Hegarty, 1988) and *P. velutina* can be seen only with a hand lens. The woody root climber, *Parsonsia straminea*, climbs only by adventitious roots in the seedling stage and begins to twine around its support as it matures. The stems of mature individuals of *P. straminea* often lose their adventitious roots and become detached from the trunk of their support tree.

TABLE 1

Number of native species and the proportion of adult individuals using each climbing mechanism at Moonabung

Main Climbing Mechanism	Number of species	Proportion of adult climber individuals (%)
Twiners	19	69
Root climbers	2	17
Tendrill climbers	4	13
Scrambler/hook	1	1

Support Stem Thickness as a Constraint for Climbers

Using the present data, frequency distributions of climber presence against support-tree stem diameter at breast height have been drawn up for twiners, tendrill climbers and root climbers in turn (Fig. 2). A distinction has been made between climber stems less than 1.0 cm in diameter and those equal to or greater than 1.0 cm. It seems reasonable to assume that all or most members of the former group have only recently begun to climb.

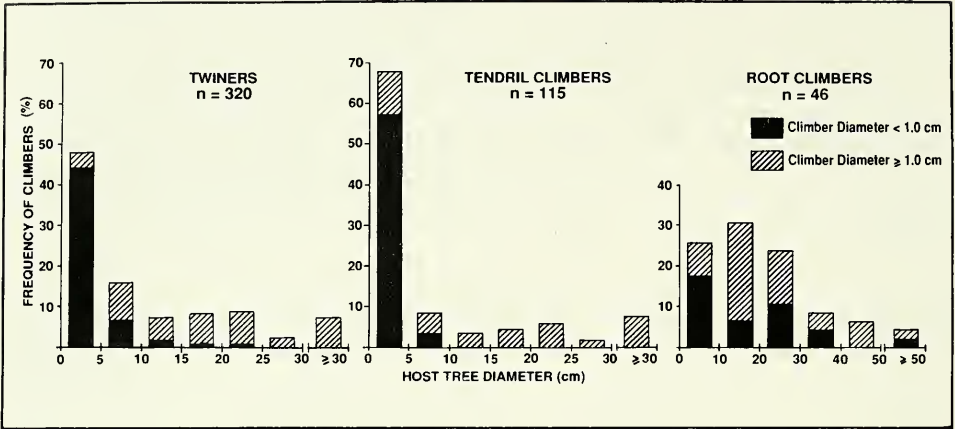


Fig. 2. Frequency distributions of climbing plants (twiners, tendrill climbers and root climbers separately) on supports of different stem diameters (at breast height).

Twiners and tendrill climbers are unable to climb supports with large diameters. Most young twiners occur on supports of less than 10 cm diameter, most young tendrill climbers occur on supports of less than 5 cm diameter. On the other hand, root climbers of stem diameter less than 1cm are present on a wide range of support-stem diameters.

It might be expected that, for the twiners and tendrill climbers, climber and support stem diameters would be positively correlated. This expectation is borne out when product-moment correlation coefficients are calculated for the data on which Fig. 2 is based (for twiners, $r = 0.65$, $p < 0.01$; for tendrill climbers, $r = 0.73$, $p < 0.01$). For the root climbers, however, the calculated correlation coefficient ($r = 0.18$) is not significantly different from zero at the 1% probability level.

Horizontal Extent

The results of measurements of direct distance from the nearest rooting point to the base of the next support are shown in Fig. 3 for the ten most abundant liane species. This measurement gives an indication of the capability for local spread. Figure 3 indicates that *Morinda acutifolia* (F. Muell. ex Benth.), *Parsonsia velutina* and *Jasminum volubile* Jacq. are fairly restricted and are generally limited to supports 1-2 m away from a rooting point. Observations indicate that stems of *Cissus antarctica* F. Muell. Vent., *Tetrastigma nitens* (F. Muell.) Planch. and *Malaisia scandens* subsp. *scandens* tend to ramble extensively over the shrub and small-tree layer. In contrast, horizontal spread near the tops of canopy trees is common for *Austrosteenisia blackii*, *Legnephora moorei*, *Pandorea pandorana* (Andr.) Steen. and *Parsonsia straminea*. Of these, *Parsonsia* produces twining leaders which can spread between support crowns and remain established there even if the initial support (climbed with adhesive roots) has fallen. Thus, *P. straminea* differs from most other root climbers, which depend on adhesive roots only; the latter have previously been noted as being unable to spread to neighbouring supports (Darwin, 1875; Hegarty, 1988). No other root-climber lianes were observed at Moonabung Falls.

Most lianes at Moonabung have self-supporting leading shoots which generally point in an upward direction. Putz (1984a) commented that the distance that a liane can traverse between supports is determined by the length of the stem it can hold erect out of the top of a support. *Cissus antarctica* has relatively rigid, thick, self-supporting (to a certain length) leaders and these usually point in a more upward direction than the

leaders of *Tetrastigma nitens*. This observation may partially explain the large difference apparent in Fig. 3 between these two tendril climbers.

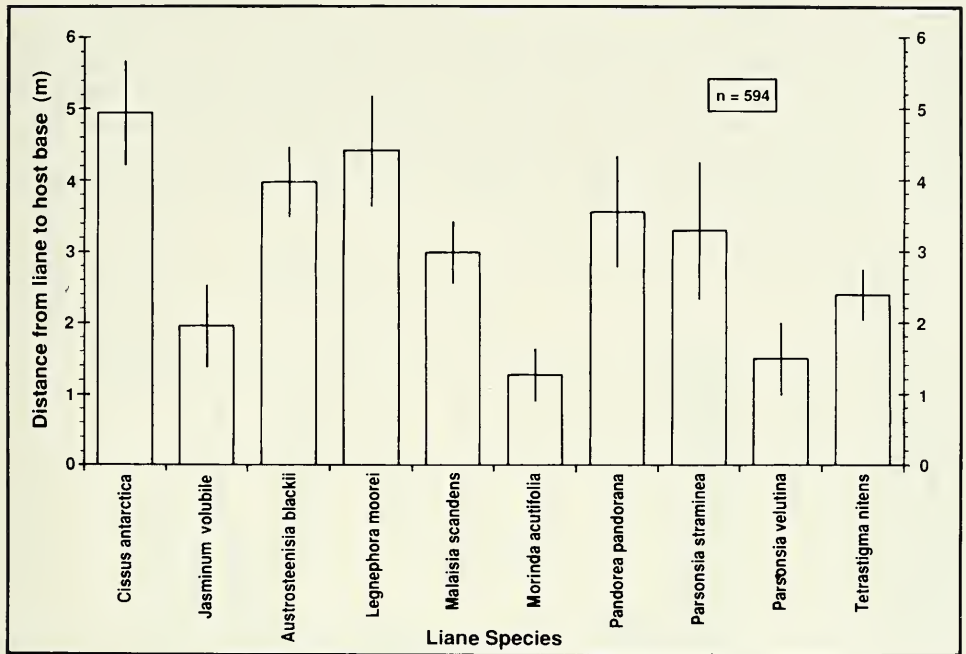


Fig. 3. Direct distance along the ground from each liane rooting point to the base of the next support along the stem. Values are mean distances for adult climber individuals (vertical bars are 95% confidence limits).

Most climbers are supported by more than one support and the average number of supports (no lower dbh limit) per individual of all the climber species (lianes and thin wiry) observed at Moonabung, was 3.9 (standard error = 0.28, $n = 174$). The greatest number of supports — twenty-three — was recorded for an individual of *Malaisia scandens* subsp. *scandens*; about half of them were < 4m in height.

Seedlings and Vegetative Reproduction

The relative frequencies of liane seedlings observed in the Moonabung rainforest stand are shown in Fig. 4. The greatest number of seedlings was produced by *Jasminum volubile* (32% of the total), while seedlings of *Parsonsia velutina* and *Parsonsia straminea* were also relatively common. No seedlings of *Legnephora moorei* (F. Muell.) Miers and *Cissus antarctica* were seen at Moonabung even within gaps; Hegarty (1988) noted in her study that none of the fruits of these two species were observed to germinate in the rainforest stand at Mt. Glorious, even towards its edge. However, the sampling period at Moonabung occurred during severe drought conditions, a fact which should be kept in mind when considering the seedling patterns observed there.

Regardless of their ability to produce seedlings beneath a closed canopy, most of the liane species at Moonabung can reproduce vegetatively. The potential for vegetative regeneration is demonstrated in Fig. 5 by the mean number of secondary rooting points per plant for the ten main liane species. Because of the large 95% confidence limits for certain species, only tentative conclusions can be made. However, it is apparent that some of the lianes (*Parsonsia velutina*, *Parsonsia straminea*, *Pandorea pandorana*, *Jasminum*

volubile and *Morinda acutifolia*) are less likely than the others to form secondary rooting points. There is a significant negative correlation (Spearman rank correlation coefficient, $r_s = -0.59$; $p < 0.05$) between the mean number of rooting points per individual for each liane species and the logarithm of the number of seedlings observed for that species. Such a correlation implies that species with a low potential for vegetative reproduction produce a greater number of seedlings than those species with a high potential for cloning. The data in Fig. 5 suggest that both *Legnephora moorei* and *Cissus antarctica* are readily able to reproduce vegetatively. This characteristic may allow their long-term persistence in the stand despite the competitive threat posed by *Lantana camara* which, because it dominates the larger canopy gaps, may seriously inhibit the seedling regeneration of these two lianes.

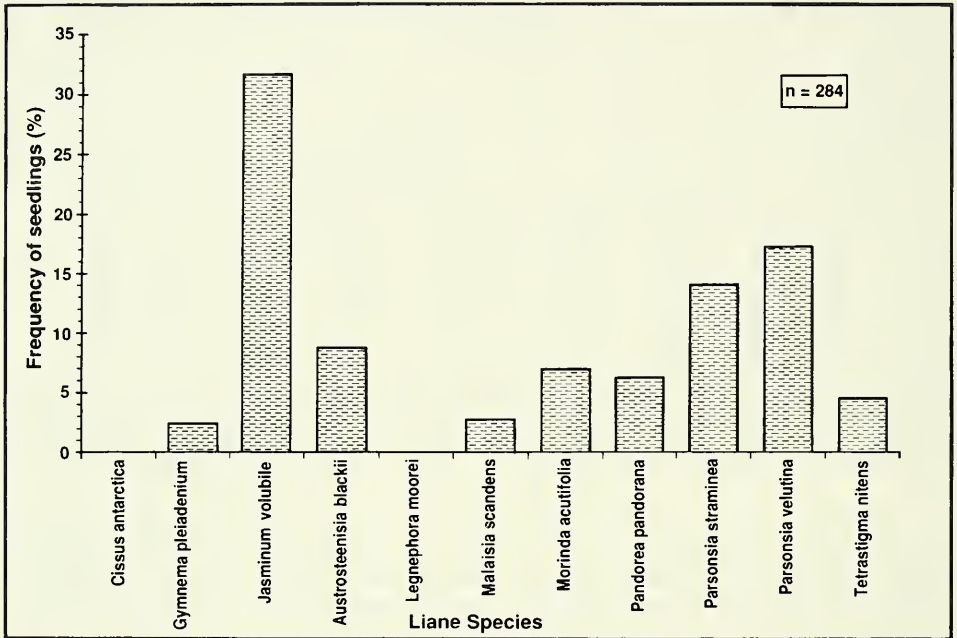


Fig. 4. Relative numbers of liane seedlings observed within the Moonabung rainforest stand. Only the most abundant species are included (refer to Appendix).

Vertical Distribution

The vertical distribution of adult climber individuals (regardless of species) within the rainforest stand at Moonabung is illustrated in Fig. 6. Because climbers generally occur on a number of supports in reaching their preferred position, each individual in Fig. 6 has been included only in the highest zone reached by it (following the approach of Grubb et al., 1963). Stratification of climber individuals within the rainforest structure is apparent, with two main peaks being recognised. The lower peak of climber individuals at 2 to 4 m represents the thin wiry (shade-tolerant) climbers, which seldom grow higher than the shrub and small-tree layer or which occur on rock-faces. A large proportion (70%) of climbers is found in the upper layer (6 to 16 m), with a peak in the 10 to 12 m height zone, and this group consists wholly of lianes. The wide range of heights occupied by lianes in the upper layer is presumably due to slight differences in preferred heights between species, to unevenness in tree canopy height and to the presence of some climbers still actively climbing towards their preferred position.

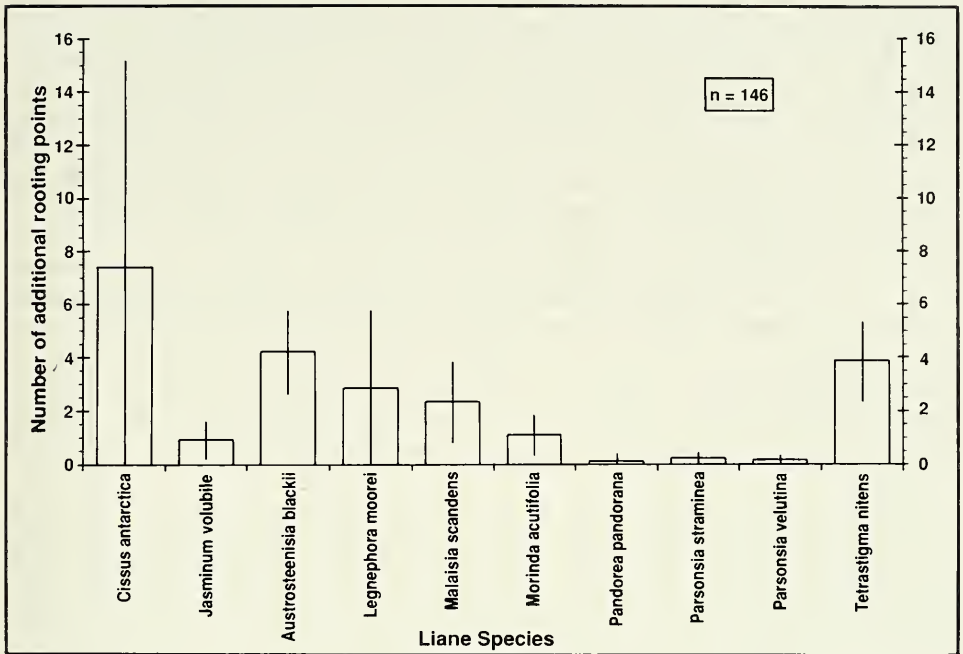


Fig. 5. Number of secondary rooting points for the most abundant liane species. Values are means per adult liane individual (vertical bars are 95% confidence limits).

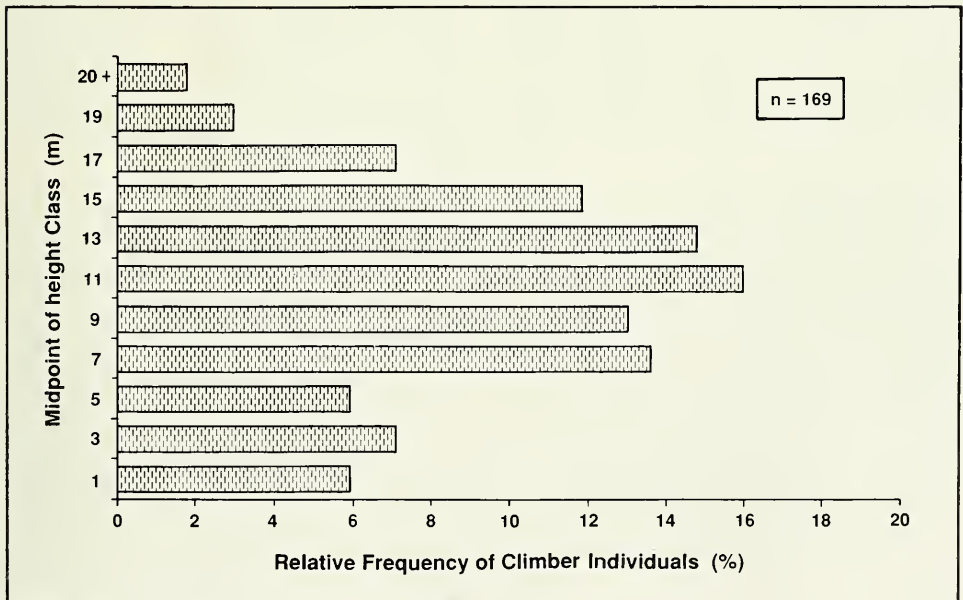


Fig. 6. Vertical distribution of adult climber individuals (all species combined) within the Moonabung rainforest stand. Each individual has been included only in the highest zone it reached. Height (above the ground) classes are 0-1.9m, 2.0-3.9m, 4.0-5.9m etc.

The decrease in the number of climber individuals in the 16 to 20+ m height zone is mainly due to the corresponding decrease in the number of available supports at these heights, i.e. the canopy generally ranges in height from 14 to 18 m with only scattered emergents present up to 25 m. Further, the relatively low number of individuals in the 0 to 6 m height zone reflects the sparseness of the shrub and small-tree layer within the Moonabung rainforest stand. The minor peak at the 6 to 8 m height zone may correspond to the discontinuous small-tree layer mentioned previously. The stratification of climber individuals at Moonabung is, to some degree, related to the vertical abundance of supports.

The vertical distribution of each of the main liane species is shown in Fig. 7. Means (and 95% confidence limits) are presented of the maximum height of adult climber individuals on each support they encountered. Three groups of species can be distinguished. Light-demanding species, typically found at the top of canopy trees, are represented by *Austrosteenisia blackii*, *Legnephora moorei*, *Pandorea pandorana* and *Parsonsia straminea*. Shade-tolerant species, typically found in the shady environment at intermediate heights, are represented by *Morinda acutifolia*, *Parsonsia velutina* and *Jasminum volubile*.

The third group consists of species with extensive shoot systems that use the shrub and small-tree layers to climb progressively towards their preferred position. Inclusion of the heights at which these actively-climbing branches are found (on shrubs and small trees) in the calculations, resulted in the overall mean maximum height being lower than the final preferred position (assumed to be the maximum height of the main stem). In the case of *Tetrastigma nitens* and *Cissus antarctica* this preferred position was at the top of the canopy and for *Malaisia scandens* subsp. *scandens* it was an intermediate-to-canopy-top position.

In general, there is little variation between the liane species in the relative vertical position they occupy on their support; most are found in the top 30% of their support (i.e. 70% to 100% of the support height). Thus, shade-tolerant liane species, indicated in Fig. 7 as occurring at intermediate heights, are occupying positions at the top of small or medium-sized trees and the light-demanding species are generally found towards the top of canopy trees. Presumably, light intensity is greater in the top 30% of the support tree, and this is advantageous to both shade-tolerant and light-demanding species.

Support Preferences

To determine whether climbing plants demonstrate a preference towards particular support tree species, the number of individuals observed as supports was compared with the number of individuals expected to be acting as supports. Assuming that each support individual has an equal chance of being invaded by a climber then the number expected as supports for each tree species should have the same distribution as the overall tree population. Relative densities of tree species at Moonabung, from which the numbers of individuals expected as supports were calculated, were obtained from S. Vernon (unpublished data) and are presented in Table 2. The number observed as supports included only those of adult climbers, to ensure that successful invasions of supports were being considered. Further, only support trees ≥ 10 cm gbh were included to make the data of the present study comparable with those of Vernon.

There is a significant difference between the observed and expected frequencies (chi-squared value = 95.9, $p < 0.001$) suggesting that, overall, climbing plants demonstrate support preferences. Table 2 indicates for instance that climbers show a preference towards *Streblus brunonianus*. This tree may be a favourable support because of its small leaf-size and sparse foliage which may reduce competition for light between the climber foliage and the foliage of its support. Further, its relatively low, much-branched

crown may well make it accessible to climbers. The results suggest that spines on the trunk and branches of *Capparis arborea* do not reduce its susceptibility to climber invasion, there being little difference between the observed and expected numbers. This observation also supports those of Putz (1984b) for similar trees in a tropical moist forest in Panama. There was a low frequency of climbers on the small trees *Cleistanthus cunninghamii* Muell. Arg. and *Alchornea ilicifolia* (J. Smith) Muell. Arg., possibly because there are few climber species whose preferred position (and therefore support) is in the understorey. *Baloghia inophylla* (Forst. f.) P. Green has relatively large leaves and a particularly dense crown and these characteristics may partially explain the trend away from this species. *Mallotus philippensis*, the most abundant tree species at Moonabung, was also not favoured but the reason for this is not readily apparent.

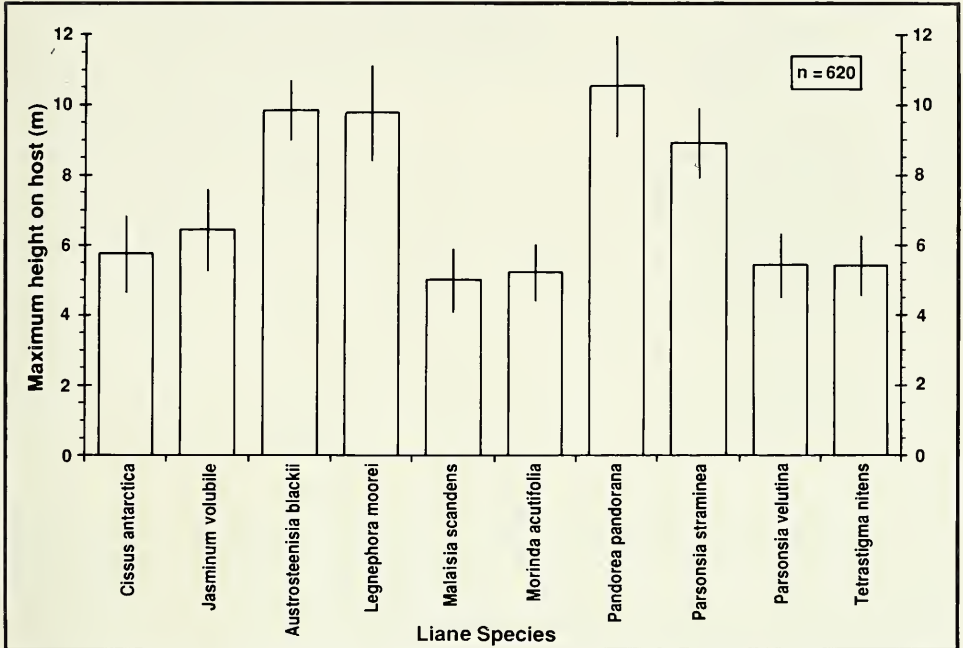


Fig. 7. Vertical distribution of the ten most abundant liane species within the Moonabung rainforest stand. Values are mean maximum heights of adult climber individuals (vertical bars are 95% confidence limits).

Table 2 indicates that the frequency of climbers on the less common species within the stand (i.e. the remainder of the tree species) is greater than expected. Such a trend is difficult to interpret, but may be partially due to the fact that seven of the twenty-seven plots from which Vernon (1985) determined overall relative tree density were located on the southern side of Webbers Creek, which was not sampled in the present study. For this reason, the support preference data should be interpreted with caution and differences in support preference between individual climber species will not be examined here. However, it is possible that inter-specific differences in support preference amongst climbers do occur as a result of differences in the position they occupy in the vertical structure of the rainforest and in their climbing characteristics.

DISCUSSION

Patterns of Vertical Distribution

The way in which climbing plants fit into the three-dimensional structure of the rainforest stand is related both to the disposition of trees and shrubs and to the growth

characteristics of the climbers themselves. In the Moonabung Falls stand the shrub and small-tree layer is sparse and discontinuous and the number of adult climbing plants within this height-zone is relatively low. Generally, thin wiry climbers occupy this part of the understorey and these climbers are few in number and in species here.

TABLE 2

A comparison between the observed and expected number of trees (≥ 10.0 cm gbh) of each species acting as climber supports at Moonabung

Expected number of support trees calculated from Vernon's unpublished data — see text for explanation. Chi-squared value = 95.9, $p < 0.001$.

Host Species	Number of Trees Observed as Hosts	Number Expected as Hosts
<i>Mallotus philippensis</i>	95	121
<i>Drypetes australasica</i>	68	49
<i>Streblus brunonianus</i>	77	48
<i>Cleistanthus cunninghamii</i>	27	42
<i>Capparis arborea</i>	31	34
<i>Dendrocnide photinophylla</i>	22	28
<i>Baloghia inophylla</i>	20	43
<i>Olea paniculata</i>	34	29
<i>Brachychiton discolor</i>	10	17
<i>Dendrocnide excelsa</i>	7	16
<i>Sarcomelicope simplicifolia</i>	18	9
<i>Alchornea illicifolia</i>	1	9
<i>Croton verreauxii</i>	9	7
<i>Elattostachys nervosa</i>	5	6
Remainder of tree species	91	57
Total	515	515

The foliage of most climbers is found within a broad zone encompassing the crowns of the medium and large trees of the uneven canopy layer. Lianes are characteristic of this zone and the wide range of heights occupied here is partially due to differences in preferred heights between liane species. Shade-tolerant lianes, such as *Parsonsia velutina*, *Morinda acutifolia* and *Jasminum volubile*, occupy positions at intermediate heights, while the light-demanding lianes occur towards the top of the canopy. These light-demanding species are *Austrosteenisia blackii*, *Legnephora moorei*, *Cissus antarctica*, *Tetrastigma nitens*, *Pandorea pandorana* and *Parsonsia straminea*. Above this broad zone, the number of climbers decreases as the number of available supports decreases, until only scattered emergent trees are present. Only light-demanding species are found in these exposed positions: the only climbers observed at the top of emergent trees were *Austrosteenisia blackii* and *Pandorea pandorana*.

The vertical position of the foliage of the lianes at Moonabung is described in Table 3 which summarises the observed growth characteristics of the individual species. There is some overlap between the four successive categories especially in the case of *Jasminum volubile*; its position ranges from the top of the crown of small trees to very occasionally the inner crowns of large trees.

In general, the shade-tolerant species found at intermediate heights (*Morinda acutifolia*, *Parsonsia velutina* and *Jasminum volubile*) have relatively limited horizontal spread, while the six light-demanding canopy-top species mentioned above are relatively far-ranging in their horizontal extent. Similarly, Grubb et al. (1963) observed, in montane and lowland rainforest in Ecuador, that light-demanding climbers

commonly spread from tree to tree in the canopy and tie the trees together, while the shade-tolerant climbers seldom spread from tree to tree. Perhaps there is little advantage in spread for the shade-tolerant species because photosynthetic gains would be likely to be small, due to the low light intensity in the understorey, and might not compensate for the additional investment in stems and foliage.

Characteristics of the Support

A consequence of the climbing habit is that climbers require an additional resource, i.e. a support. The climbers at Moonabung demonstrate a preference for certain support-tree species, including *Streblus brunonianus*. It is suggested that suitability as a support may be related to its leaf-size and density of foliage, as well as accessibility in terms of the degree of branching and the depth of its crown. In general, there appears to be a trend away from the larger-leaved supports (e.g. *Brachychiton discolor* F. Muell., *Dendrocnide excelsa* (Wedd.) Chew, *Mallotus philippensis* and *Baloghia inophylla*) and a preference towards the smaller-leaved supports (e.g. *Streblus brunonianus*, *Olea paniculata* L. and *Drypetes australasica*).

Most of the climbers at Moonabung were shown to require support stems of small diameter when they first begin to climb, depending on the climbing mechanism used. Most young apical twiners at Moonabung climb only on supports <10 cm in diameter; most young tendril climbers climb only on supports <5 cm in diameter. These results agree substantially with those of Putz (1984a) and Hegarty (1988) who found that tendril climbers require small-diameter supports while apical twiners can climb slightly larger supports but are also unable to climb large-diameter supports.

Thus the shrub and tree composition of the rainforest stand will strongly influence the vertical and horizontal distribution of climbers. Three of the tendril climbers present at Moonabung (*Cissus antarctica*, *Tetrastigma nitens* and *Cayratia clematidea* (F. Muell.) Domin.) were designated as early successional species by Hegarty (1988), in her study in a stand of sub-tropical rainforest in south-east Queensland. It was observed at Moonabung that these species climb the relatively small-sized supports which would be expected to be abundant in disturbed rainforest. Hegarty (ibid.) also found that root climbers belong to a later successional group, a result in agreement with the observation here that root-climbers climb a wide size-range of supports including large supports.

Three liane species in particular, *Cissus antarctica*, *Tetrastigma nitens* and *Malaisia scandens* subsp. *scandens*, make extensive use of the shrub and small-tree layer to climb a series of successively taller supports to their preferred positions. Most of the observed climbing stems of these species were branches, still dependent on the parent plant, and they spread considerable distances through the understorey (see Table 3). The fact that tendril climbers (the first two of the three species mentioned above) initially use supports of small diameters suggests that they usually step up towards the canopy, often using only temporary supports (twigs and petioles). Such a characteristic may appear fairly inefficient in terms of the distance which must be travelled to reach the canopy; however, the energy cost of production of tendrils is relatively cheap and the length of stem required to ascend to the same height is greater for a twiner than for a tendril climber (Darwin, 1875; Jaffe and Galston, 1968). Further, such a strategy may well be affordable if the branch is still attached to the parent liane so that exploration can be subsidised by the foliage already established in the canopy. *Malaisia scandens* subsp. *scandens* is the only twiner at Moonabung observed to use this strategy of climbing progressively larger supports to step up towards its preferred position.

Considering that most climbers are unable to climb large-diameter supports, two features characteristic of rainforest communities may aid in providing a diversity of favourable-sized supports. The suppressed growth of most of the saplings of canopy

species is advantageous to climbers, because such saplings provide potential supports of a suitable diameter. Disturbance of the canopy by treefalls will also increase the abundance of small-diameter supports. Since the presence of climbers increases the probability of their support tree falling (Putz, 1984a) and because climbers tie many supports together, they may (to some extent) regulate community structure to their own advantage by increasing the frequency of disturbances (i.e. treefall). A mosaic of disturbed and undisturbed areas not only provides a diversity of support-sizes but also allows maintenance of the populations of those climber species able to regenerate only in gaps.

Climber Persistence

The diameter distribution of the climber population at Moonabung (Fig. 1) shows an abundance of individuals in the smallest diameter class and a rapid decline in numbers to the second diameter class. Many of the plants in the smallest diameter class may be held there for lengthy periods because of the absence of a canopy opening above and/or the lack of a suitable support. The weakly bimodal nature of the individual frequency distributions of the more common woody species may come about if those plants which escape growth suppression on the forest floor are able to grow rapidly through the next-to-smallest size-classes, as suggested by Richards (1952) and Knight (1975). Perhaps the irregular frequency distributions shown by some of the liane species may result in part from the intermittent creation of treefall gaps.

In contrast to the observations of Penalosa (1984) in Mexico, it was found that most of the liane species at Moonabung produce shade tolerant seedlings able to regenerate in closed forest. Exceptions are *Cissus antarctica* and *Legnephora moorei*, which seem to be able to regenerate by seedlings only in gaps. Most of the liane species are also capable of vegetative reproduction, although it is apparent that some species have a greater potential for it than others (see Table 3). The widespread ability to form secondary rooting points allows the liane to be growing at the distal end while the stem at the point of initial emergence is dying off through senescence. This phenomenon has also been described by Ray (1983) for a climbing aroid in Costa Rica. He remarked that although no part of the plant (other than the apex) actually moves, the plant as a whole becomes displaced over time. The same thing probably happens with some of the lianes at Moonabung over long time periods.

The model set out by Penalosa (1984) to explain the maintenance of lianes in a stand of evergreen rainforest in Mexico seems applicable to at least some of the lianes found at Moonabung. He proposed that new liane genet (individuals produced by sexual reproduction, and therefore having a unique genetic constitution) begin growth in disturbed sites (especially treefall gaps) and, depending on the species, genet recruitment results from the germination of dormant seeds, release of shade-suppressed seedlings or increased survivorship of seeds and seedlings in clearings. As the gap closes, lianes both climb towards the forest canopy and are carried up by tree saplings. Branching of the original colonising genet results in a system of interconnected daughter canopies (ramets). These connections can become severed and the ramets can thus become entirely independent of each other. As the genet grows, its ramets flower and a seed rain is produced. A few of the seeds may reach other gaps and the whole process is repeated (Penalosa, *ibid.*). It is suggested that at Moonabung this type of behaviour may occur in those liane species which do not produce seedlings under a closed canopy (*Cissus antarctica* and *Legnephora moorei*) and in those species with superior ability to form ramets (also *C. antarctica* and *L. moorei* as well as *Malaisia scandens* subsp. *scandens*, *Tetragymma nitens* and *Austrosteenisia blackii*).

TABLE 3
Summary of overall growth characteristics of the main liane species as observed within the Moonahung Falls rainforest stand.
 Definition of small, medium and large trees is relative to the heights of trees within the stand.

	Vertical Position of Foliage	Horizontal Extent	Number of Hosts	Number of Rooting Points	Number of Seedlings	Liane Species
1.	Top of the main canopy	wide: predominantly canopy spread wide: canopy and understory spread wide: canopy and understory spread wide: predominantly canopy spread	many many many medium	many many many few	medium none none few medium	<i>Austrosterenis blackii</i> <i>Legnephora moorei</i> <i>Cissus antarctica</i> <i>Tetrastigma nitens</i> <i>Pandorea pandorana</i>
2.	Inner crowns of large trees — Tops of crowns of medium trees	wide: predominantly canopy spread wide: canopy and understory spread	few many	few many	many few	<i>Parsonsia straminea</i> <i>Malaisia scandens</i> subsp. <i>scandens</i>
3.	Mainly in the tops of the crowns of medium trees	limited	few	few	many	<i>Jasminum volubile</i>
4.	Inner crowns of medium trees Tops of crowns of small trees	limited limited	few few	few few	medium many	<i>Morinda acutifolia</i> <i>Parsonsia velutina</i>

At Moonabung the light-demanding species tend to establish daughter canopies (usually large) in the full sunlight on the tops of canopy trees. Establishment of daughter canopies by shade-tolerant lianes is not as common, with the exception of *Malaisia scandens* subsp. *scandens* for which small daughter canopies are frequent in the understorey. This species also forms small leafy canopies which sprawl over large rocks.

The advantage of the establishment of daughter canopies (ramets), and their spread in the understorey and the canopy, is considerable. Liane canopy growth is under hydraulic constraints, being ultimately limited by stem thickness; thus a liane can increase its leaf-area without excessive stem thickening (thickening being a contradiction of the climbing habit) by producing daughter canopies (Penalosa, 1984). Such a strategy also increases the expected life-span of the genet because the risk of mortality is spread over a number of ramets and the fate of the genet is uncoupled from the fate of the first tree that it climbed (Penalosa, *ibid.*).

However, the establishment and maintenance of stolon systems are costly (Penalosa, *ibid.*); for some liane species those costs may outweigh the benefits and their horizontal spread and ability to form stolons may be limited. For shade-tolerant species at Moonabung (*Morinda acutifolia*, *Parsonia velutina* and *Jasminum volubile*) both exploration and the subsequent increase in leaf-area may not necessarily be advantageous. Further, these species can probably depend on sexual reproduction to maintain their populations. Of course there is an overlap in these different strategies, but two of these shade-tolerant species (*J. volubile* and *P. velutina*) were noted to be the biggest producers of seedlings within the stand (see Fig. 4 and Table 3). The findings so far suggest that the relative importance of the two reproductive strategies used by liane species is a topic worthy of further investigation.

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References

- BRIDGMAN, H. A., 1984. — *Climatic Atlas of the Hunter Region*. Board of Environmental Studies Research Paper No. 9. Newcastle: University of Newcastle.
- CHALMERS, A. C., unpubl. — *Climbing Plants in a Dry Rainforest Community in the Lower Hunter Valley*. Newcastle: University of Newcastle, B.Sc.Hons. Thesis.
- COTTAM, G., and CURTIS, J. T., 1956. — The use of distance measures in phytosociological sampling. *Ecology* 37(3): 451-460.
- CRIBB, A. B., 1985. — The direction of twining in some Queensland plants. *Queensland Naturalist* 25 (5-6): 122-124.
- DARWIN, C., 1875. — *On the Movements and Habits of Climbing Plants*. London: Murray.
- DOYLE, G. B., unpubl. — *Strangler Figs in a Stand of Dry Rainforest in the Lower Hunter Valley*. Newcastle: University of Newcastle, B.Sc.Hons. Thesis.
- FLOYD, A. G., 1990. — *Australian Rainforests in New South Wales*. Vols. 1 and 2. Sydney: Surrey Beatty.
- GENTRY, A., 1985. — An ecotaxonomic survey of Panamanian lianes. In: D'ARCY, W. G., and CORREA, M. D. (eds) *The Botany and Natural History of Panama*: 29-42. Monographs in Systematic Botany from the Missouri Botanical Garden, Vol. 10. St. Louis: Missouri Botanical Garden.
- GRUBB, P. J., LLOYD, J. R., PENNINGTON, T. D., and WHITMORE, T. C., 1963. — A comparison of montane and lowland rainforest in Ecuador. I. The forest structure, physiognomy, and floristics. *J. Ecol.* 51: 567-601.
- HARA, K., 1987. — A categorisation of plant communities as habitats for climbing plants. *Ecological Rev.* 21 (2): 55-66.
- HEGARTY, E. E., unpubl. — *Canopy Dynamics of Lianes and Trees in Subtropical Rainforest*. Brisbane: University of Queensland, PhD. Thesis.

- , 1989. — The Climbers — Lianes and Vines. In: LIETH, H., and WEGER, M. J. A. (eds). *Tropical Rainforest Ecosystems: Biogeographical and Ecological Studies*: 339-353. Ecosystems of the World, Vol. 14B. Amsterdam: Elsevier.
- JAFFE, M. J., and GALSTON, A. W., 1968. — The physiology of tendrils. *Ann. Rev. Plant Physiol.* 19: 417-434.
- KELLY, D. L., 1985. — Epiphytes and climbers of a Jamaican rainforest. Vertical distribution, life forms and life histories. *J. Biogeog.* 12: 223-41.
- KNIGHT, D. H., 1975. — A phytosociological analysis of species- rich tropical forest on Barro Colorado Island, Panama. *Ecol. Monogr.* 45: 259-84.
- PENALOSA, J., 1983. — Shoot dynamics and adaptive morphology of *Ipomoea phillomega*, a tropical rainforest liane. *Ann. Bot.* 52 (5): 737-754.
- , 1984. — Basal branching and vegetative spread in two tropical rain forest lianes. *Biotropica* 16 (1): 1-9.
- PUTZ, F. E., 1983. — Liane biomass and leaf area of a 'terra firme' forest in the Rio Negro Basin, Venezuela. *Biotropica* 15(3): 185-189.
- , 1984a. — The Natural History of lianes on Barro Colorado Island, Panama. *Ecology* 65(6): 1713-1724.
- , 1984b. — How trees avoid and shed lianes. *Biotropica* 16(1):19-23.
- , and CHAI, P., 1987. — Ecological studies of lianes in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* 75: 523-531.
- RAY, T., 1983, Species Accounts: *Syngonium triphyllum*. In: JANZEN, D. H. (ed) *Costa Rican Natural History*: 333-335. Chicago: Univ. of Chicago Press.
- RICHARDS, P. W., 1952. — *The Tropical Rain Forest*. Cambridge: Cambridge Univ. Press.
- VERNON, S. L., unpubl. — *Dry Rainforest of the Hunter Valley: A Comparative Study*. Newcastle: University of Newcastle, B.A.Hons. Thesis.
- WEBB, L. J., 1968. — Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology* 49(2): 296-311.
- , 1978. — A general classification of Australian rainforests. *Aust. Plants* 9 (76): 349-363.
- WILLIAMS, J. B., 1979. — *A Checklist of the Rainforest Flora of New South Wales*. Armidale: University of New England.
- , HARDEN, G. J., and McDONALD, W. J. F., 1984. — *Trees and Shrubs in Rainforests of New South Wales and Southern Queensland*. Armidale: University of New England.

APPENDIX

List of climbers observed in the Moonabung Falls stand, together with the climbing mechanism(s) employed by each and their relative abundances (Importance Values [IV's], see text)

IV's were calculated only for those native climbers with at least one individual with a stem ≥ 1.0 cm diameter. *Lantana camara* is the only introduced climber.

Family	Species		Climbing Mechanism	Relative Abundance (IV) %
Apocynaceae	<i>Parsonia straminea</i>	(R. Br.) F. Muell.	root climber + apical twiner	15.9
	<i>Parsonia velutina</i>	R. Br.	apical twiner + minute hooks	7.9
Asclepiadaceae	<i>Gymnema pleiadenium</i>	F. Muell.	apical twiner	2.4
	<i>Marsdenia flavescens</i>	Cunn.	apical twiner	
	<i>Tylophora barbata</i>	R. Br.	apical twiner	
Bigononiaceae	<i>Pandorea pandorana</i>	(Andrews) Steenis	apical twiner	8.1
Celastraceae	<i>Celastrus australis</i>	Harvey & F. Muell.	apical twiner	
Cunoniaceae	<i>Aphanopetalum resinosum</i>	Endl.	apical twiner	
Davalliaceae	<i>Arthropteris tenella</i>	(Forster. f.) J. Smith	root climber (epiphyte)	
Dioscoreaceae	<i>Dioscorea transversa</i>	R. Br.	apical twiner	
Fabaceae	<i>Austrasteenisia blackii</i>	(F. Muell.) Gees.	apical twiner	23.7
Menispermaceae	<i>Legnephora moorei</i>	(F. Muell.) Miers	apical twiner	4.3
	<i>Sarcopetalum harveyanum</i>	F. Muell.	apical twiner	
Moraceae	<i>Maclura cochinchinensis</i>	(Lour.) Corner	scrambler + hooks	1.1
	<i>Malaisia scandens</i> subsp. <i>scandens</i>	(Lour.) Planchon	apical twiner + minute hooks	6.3
Myrsinaceae	<i>Embelia australiana</i>	(F. Muell.) Mez	apical twiner	1.7
Oleaceae	<i>Jasminum volubile</i>	Jacq.	apical twiner	8.3
Ranunculaceae	<i>Clematis glycinoides</i>	DC	twining petioles	
Rubiaceae	<i>Morinda acutifolia</i>	(F. Muell. ex Benth.)	apical twiner	7.4
		F. Muell.		
Smilacaceae	<i>Eustrephus latifolius</i>	Ker Gawler	apical twiner	
	<i>Geitonoplesium cymosum</i>	(R. Br.) R. Br.	apical twiner	
	<i>Ripogonum album</i>	R. Br.	apical twiner + prickles	0.4
Verbenaceae	<i>Lantana camara</i>	L.	scrambler + prickles	
Vitaceae	<i>Cayratia clematidea</i>	(F. Muell.) Domin	tendrill climber	
	<i>Cissus antarctica</i>	Vent.	tendrill climber	3.7
	<i>Cissus opaca</i>	F. Muell.	tendrill climber	
	<i>Tetrastigma nitens</i>	(F. Muell.) Planchon	tendrill climber	8.8

100.0